Do humans forage optimally and what does this mean for zoology on the table?

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ABSTRACT

Optimal Foraging Theory (OFT), enables understanding of foraging behaviour, which is exhibited by all of life, through the assumption that foraging behaviour maximises some currency of foraging.

OFT has been relatively successful for nectar-feeding animals, with energy the primary foraging currency, and less successful for generalist herbivores and omnivores, for which foraging currencies include nutrients. It has been extended to other areas of biology, applied to human foraging, is a strong ecological theory, and 2016 marks its' 50th birthday.

Human foraging has been affected by inter-related, recent and rapid developments of agriculture, animal husbandry, technology, social living and culture. Consequently, the foraging environment in which humans evolved is long gone, and our foraging may not be well adapted to current circumstances.

Human foraging is therefore caught in "evolutionary traps". For example, as generalist omnivores we evolved a 'balanced diet', commonly represented by 'food pyramids', reflecting how often we encountered and consumed various food types during our evolutionary past. We therefore evolved preferences to collect and consume foods high in fats, oils, sugar and salt, valuable when rare, but adversely affecting our health with increasing availability. Additionally, given diverse arrays of potential food items, we should mimic foraging behaviour of others, especially those we know, admire and trust. Consequently, we are strongly affected by cultural influences, and by advertising and marketing of food types and 'fad diets', especially when promoted by movie stars, sports heroes and the like.

Being omnivores, animal meat will likely remain 'on the table' indefinitely, with consumption depending on availability, plus benefits and costs, whether real or imaginary, all ingredients of the optimal foraging approach. Of course, perceived benefits of consuming animal meat are likely to be greatly influenced through what we hear or see via others.

Looking ahead, 'zoology on the table' will remain contentious, OFT will be significantly developed for non-human organisms with some interest in understanding human foraging, and there will be much further research on effectiveness of advertising. No doubt, we shall continue to be deluged with messages advocating what we should eat and drink, and health issues associated with non-optimal diets will persist.

Key words: human; foraging; diet; optimal foraging theory; advertising; culture; evolutionary trap; health; generalist omnivore

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Introduction

In the context of human foraging, 'zoology on the table' has been a contentious issue, providing ample justification for our present forum (Lund and Olsson 2006). For my part in this discussion, I take 'zoology on the table' to include the collection and eating of any organism that is a member of the animal kingdom. Such organisms include many food types that we humans commonly eat, such as birds, mammals, and fish, all of which are vertebrates, as well as certain invertebrates such as molluscs (e.g., mussels, scallops, oysters), crustaceans (e.g., crabs, lobsters, crayfish) and cephalopods (e.g., squid, octopus). Less commonly eaten animals include amphibians (e.g., frogs), reptiles (snakes, lizards) and various insects. We humans rarely eat members of other animal groups such as annelid worms (Marconi *et al.* 2002) and echinoderms (Pereira *et al.* 2013), and some animal groups barely feature if at all (e.g., Poriferaor sponges; Cnidaria or anenomies, corals and jellyfish; Platyhelminthes or flatworms; Nematodes or roundworms).

Views regarding the merits of having 'zoology on the table' have varied greatly (e.g. Boada *et al.* 2016; Cabrera and Saadoun 2014; Font-i-Furnols and Guerrero 2014; Leroy and Praet 2015; Mathijs 2015), but have not previously included a perspective based on Optimal Foraging Theory. I provide such a perspective here.

In this article I provide an introduction to Optimal Foraging Theory, as a means by which we understand foraging behaviour, including that exhibited by humans, then describe relevant circumstances affecting human foraging, relate all of this to the issue of 'zoology on the table', and close with some thoughts regarding 'where to from here?'.

Optimal Foraging: An introduction

Foraging is any behavioural activity that affects intake of food, or some other resource; it involves continuous decision-making, use of information about both the past and the present, and is subject to constraints (Pyke 2010b). We generally think of foraging as including activities such as searching or hunting for food and consuming/ digesting food, but this is logically equivalent to similar activities involving any other kind of resource. In the case of humans, for example, foraging could be taken to include scrolling the internet for relevant or useful information, or even online dating. A foraging individual should be aware of where it has been, its previous foraging success, other aspects of its foraging history, and how it is presently doing, and all of this should inform its decisions regarding future foraging options. As an individual can always choose to stop what it is doing and do something different, decisions regarding foraging, or any other aspect of behaviour, must be made continuously. In general, foragers cannot alter their physical attributes such morphology and physiology, may be restricted to foraging in relatively nearby areas, and may have only certain times effectively available for foraging (e.g., day or night; high or low tide); these are all constraints that determine foraging choices and outcomes.

Foraging occurs throughout all of life, is very important, and so warrants understanding. All organisms require some resource, or food, upon which depend survival, growth and reproduction, utilise information about previous foraging (i.e., exhibit foraging memory), and alter their behaviour in response to circumstances. In other words, all life forages. Foraging often occupies much of an individual's time and features, directly or indirectly, in many interactions between individuals, populations and species. In other words, foraging is an almost ubiquitous process.

Evolutionary theory helps us to understand foraging behaviour (Pyke 2010b). Foraging behaviour, or more accurately the mechanisms and processes that determine it, would have evolved by natural selection, becoming adaptive in the sense that it confers higher biological fitness (i.e., ability to reproduce) to individuals than certain evolutionarily feasible alternatives. It might reasonably be argued, for example, that lions have evolved to do better on a carnivorous diet than they would as herbivores, and so would be expected to exhibit carnivory rather than herbivory. In this manner, many aspects of foraging, and related physical attributes, may be viewed as adaptations. Optimal Foraging Theory (OFT) further provides a potentially powerful tool for understanding foraging behaviour through the additional assumption that foraging behaviour is maximally adaptive (Pyke 1984; Pyke 2010b). In this case, it is generally assumed that the fitness outcomes of foraging can be assessed in terms of some currency, such as energy or nutrients, and that foraging maximises this currency (Simpson *et al.* 2004). This approach leads to testable predictions, both qualitative and quantitative, that are not otherwise possible. Of course, in some situations, it may be judged that an individual's 'inclusive fitness', based on genetic relatedness to other individuals, should be maximised, thus expanding the relevant evolutionary unit with regard to foraging to include kin (Breed 2014; Smith 2014). This would obviously apply to social insects, such as bumblebees and honeybees, and to humans (Mateo 2015).

OFT has been most successful with regard to nectar-feeding animals, for which the currency of foraging may often be primarily energy, and less successful for other animals, such as generalist herbivores and omnivores (Pyke 2010b; Simpson *et al.* 2004). In the case of bumblebees, for example, individual foragers are non-reproductive members of colonies consisting mostly of mother and sisters, often forage almost entirely for floral nectar, a sugar solution that provides important energy, and are not subject to predation or other factors while foraging (Pyke 1978; Pyke 1979). For these and similar reasons, it has often been hypothesised, with good success, that such nectar-feeding animals will forage in ways that maximise individual net rate of energy intake (Pyke 1981a; Pyke 1981b; Pyke 2010a). The situation is more complex with foraging behaviour of generalist herbivores, such as the much-studied moose, but, even here, the optimal foraging approach has been reasonably successful (Belovsky 1994). Few such studies have so far attempted to deal with generalist omnivores, such as humans (Simpson *et al.* 2004).

As expected, OFT has been more successful in terms of developing and testing qualitative predictions concerning foraging, than in doing so quantitatively (Pyke 2010b). For example, predictions such as an animal should prefer food type A over type B, or should expand its diet with decreases in overall food abundance, have often been quite successful. On the other hand, more precise and quantitative predictions, such as an animal should ***always*** choose to eat certain food types when encountered and ***never*** eat other food types, have rarely if ever been successful. Of course, it is not difficult to explain such downfalls of OFT, based on issues such as imperfect available information and sampling necessary to follow possible changes to circumstances, leading to further refinement and testing of predictions. In this way, OFT has developed like any other theoretical approach.

OFT has also proven useful in other areas of biology, extending beyond foraging behaviour to areas where foraging is an important component, may be considered a strong ecological theory, and is enjoying its 50th birthday in 2016. Plant pollination, for example, often involves behaviour of pollinating animals as they forage for nectar (or other floral resources) and this foraging behaviour is generally influenced by the levels of nectar encountered by the pollinators, which are in turn influenced by patterns of nectar production by the plants. In order to understand the evolution of patterns of nectar production, it is therefore necessary to include and understand pollinator foraging behaviour in relation to encountered nectar levels in flowers (Pyke 2010a). The overall success of OFT, in its own right and as it has been incorporated into such additional areas of biology, has led some to consider it a 'strong ecological theory' (Marquet *et al.* 2014). As OFT essentially began in 1966, with the classical articles by Robert Macarthur, Eric Pianka and J. Merritt Emlen (Emlen 1966; MacArthur and Pianka 1966), 2016 marks the 50th Anniversary of these initial publications.

Human foraging

Human foraging, as with foraging by any kind of animal, has always involved choice of foraging location, timing and duration of foraging in different locations, which items to eat (or collect for subsequent eating), and pattern of movements within and between locations. We (humans) choose where to hunt, fish, collect fruit, and so on. Throughout our history we would have acquired food from a variety of locations, each providing a range of food types, with visits to different locations in one sequence or another, and with varying amounts of time spent in each location. Of course, we have also sought and utilised other resources. In other words, humans have always foraged for food and other resources.

However, human foraging has, for the majority of us, been greatly affected by the inter-related, recent, and rapid developments of agriculture, animal husbandry, technology, social living and culture (Hockett 2015; Whitehouse and Kirleis 2014). Prior to the 'agricultural revolution', we probably existed in relatively small groups (i.e., about 150 individuals; Aiello and Dunbar 1993), obtaining food by 'hunting and gathering', with the aid of simple tools. Now, many of us live in towns and cities, and obtain food by driving to the supermarket. Much technology is now employed in the production, transportation and storage of food. Additionally, whether through religion, 'fad diets' or other aspects of culture, our choices of which food types to acquire and consume are affected (Hockett 2015; Simpson *et al.* 2015).

The circumstances under which human foraging evolved were therefore generally quite different to relatively recent and current circumstances (Birch 1999), and changes to our foraging environment are ongoing, sometimes at what seems to be an amazing rate. For example, the 'agricultural revolution', when we changed from being 'hunter-gatherers' towards being 'agro-pastoralists', occurred about 10 thousand years ago (Beja-Pereira *et al.* 2006; Lev-Yadun *et al.* 2000), a short time relative to our roughly 2-3 million year history (Fuentes 2015; Marean *et al.* 2015; Sayers and Lovejoy 2014). Of course, our foraging circumstances would have changed prior to the 'agricultural revolution' with changes in the earth's geology, climate and biodiversity, but such changes were presumably relatively slow. Obviously, our foraging environment has changed rapidly since the agricultural revolution, and seems now to be changing at an ever increasing rate (Raubenheimer *et al.* 2015). I see frequent changes to what food types are available (in my supermarket), as well as how they are packaged, marketed and presented, at weekly, if not daily, intervals. I see similarly frequent variation in the diets we are exhorted to adopt, as dietary recommendations are presented in magazines, on radio and television, through 'social media', and so on, often endorsed by one or other 'celebrity' or high-profile person (Feasey 2006; Kissling 1995; Pitt 2016). Not surprisingly, such diets often become 'fads' (Simpson *et al.* 2015) and may come and go quite quickly. Our foraging environment is getting further and further from what it used to be.

The foraging environment to which most of us humans biologically evolved is therefore long gone, and we cannot expect our foraging behaviour to be necessarily well adapted, in a biological sense, to our current circumstances, let alone to what they will be like in years to come (Hockett 2015). Assuming that human generation length has never been less than about 20 years (Sanford *et al.* 2015), there has only been time since the advent of agriculture for at most about 500 generations, which should allow for biological adaptation to variation in foraging environment, but presumably only in situations where changes to the foraging environment arose early during this period and have been persistent. Current differences among human ethnic groups in terms of lactose tolerance probably provide an example, where human populations that consumed dairy milk tended to evolve the ability to properly digest lactose (Pyke 1987).

It is, however, most likely that we humans have always been generalist omnivores (Marean *et al.* 2015) and have consequently evolved what we often consider to be a 'balanced diet' (Simpson *et al.* 2004) as a biological adaptation to such omnivory. It is possible, for example, that we evolved our abilities to consume and digest different food types in proportion to how frequently we encountered them, with the most frequently encountered food type being what is generally referred to as 'fruit and vegetables', followed decreasingly by 'grains' (originally seeds of various plants), then 'meat and other sources of protein', and finally various sources of fats, oils, sugar and salt (Altamirano Martinez *et al.* 2015; Phillips *et al.* 2013). If this were the case, then we would probably have evolved to do best in biological terms (i.e., survival, growth, reproduction) on what is generally considered a 'balanced diet', as reflected in

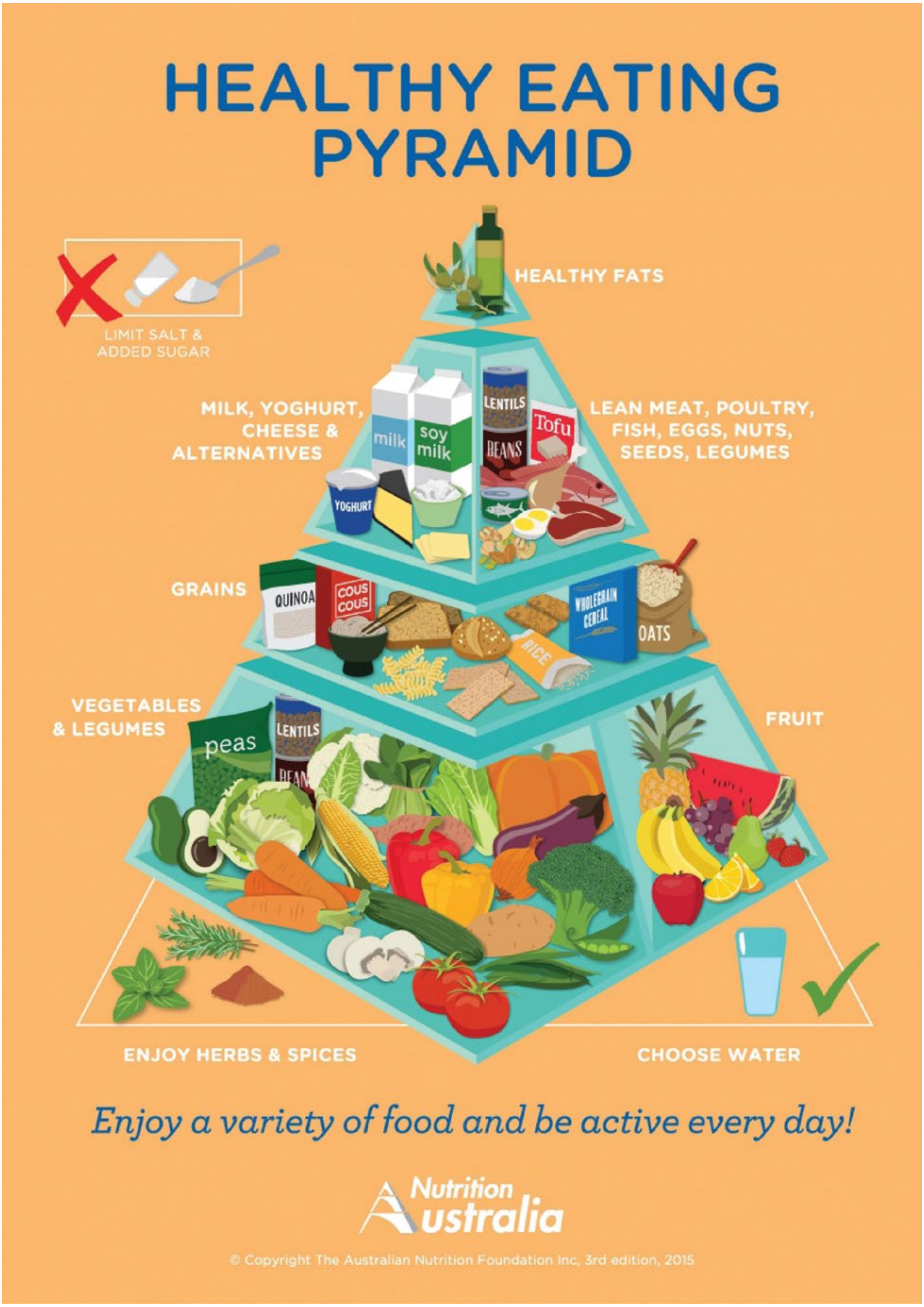
HEALTHY EATING PYRAMID
LIMIT SALT & ADDED SUGAR
HEALTHY FATS
MILK, YOGHURT, CHEESE & ALTERNATIVES
milk
soy milk
YOGHURT
LENTILS
BEANS
Tofu
LEAN MEAT, POULTRY, FISH, EGGS, NUTS, SEEDS, LEGUMES
GRAINS
QUINOA
COUS COUS
WHOLEGRAIN CEREAL
OATS
RICE
VEGETABLES & LEGUMES
peas
LENTILS
FRUIT
ENJOY HERBS & SPICES
CHOOSE WATER
Enjoy a variety of food and be active every day!
Nutrition Australia
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Figure 1: Example of a 'food pyramid' recommending relative quantities of different food types for a 'balanced' and 'healthy' human diet (produced by the Australian Nutrition Foundation, 3rd edition, 2015; http://nutritionaustralia.org/sites/default/files/HealthyEatingPyramid.jpg; accessed July 2016)

'food pyramids' (e.g., Figure 1), as are often presented in sensible (to me, at least) discussions of recommended human diets (Phillips *et al.* 2013).

A corollary of this is that we have probably evolved abilities to detect fats, oils, sugar and salt in available food types, and strong preferences to collect and consume such food types when available, resulting in significantly negative consequences to our current general state of health and well-being (Birch 1999; Savage *et al.* 2007). Many of us, myself included, have what has been called a 'sweet tooth' and are powerfully attracted to food types rich in sugar, resulting in consumption levels probably much higher than those we evolved with. Such high consumption levels of food types rich in fats, oils, sugar and salt have been linked to a myriad of health maladies including obesity, cardiac disease, and diabetes, just to mention a few on what is clearly a very long list (Lopez and Knudson 2012; Raubenheimer *et al.* 2015). In terms of our diet, we seem caught in an 'evolutionary trap', victims of our evolutionary past.

We should also have evolved strong tendencies to observe and mimic the foraging behaviour of others, especially those we know, admire, and trust, leading to another 'evolutionary trap' in the way we deal with advertising and marketing of food types. Given the obvious variation and complexity that has always existed in our foraging environment, we should have evolved to observe and mimic the foraging behaviour of our parents (Birch 1999; Savage *et al.* 2007), as they have obviously reached maturity and had us as offspring, and they would be expected to point us towards beneficial food types. We should also have evolved to follow the foraging habits of others, especially those, like our parents, who are genetically closely-related to us, and those we otherwise admire or trust to guide foraging in our best interests. An obvious consequence of the latter is that we tend to believe what we hear, read and see about desirable foraging behaviour (Pellai *et al.* 2012), especially when presented by people such as movie 'stars', television 'personalities' or sporting heroes (Feasey 2006; Kissling 1995; Pitt 2016). In this vein, it may be no accident that we rarely if ever see food adverts presented by well-known politicians, sales persons for real estate or used cars, lawyers, or university professors. In other words, food advertising and marketing 'works', and is therefore employed *ad nauseam* (to me, at least) because we trust those presenting to us, and this constitutes another 'evolutionary trap' that affects our foraging.

Human dietary choices are therefore likely to be biologically adaptive, possibly even consistent with OFT, when available foods and factors influencing dietary choice may be considered 'natural', but such situations are difficult to achieve. When foraging is observed for humans currently living as hunter-gatherers, presumably under conditions that have persisted for long periods of time, observed diets are generally consistent with OFT expectations (Alvard 1995; de Boer *et al.* 2002; Pate 1986; Thomas 2007a; Vickers 1994). However, the costs and benefits of choices between very different kinds of food, such as between meat and plant material, cannot be expressed solely in terms of energy (i.e., calories) (Hill 1988; Hockett 2015; Raubenheimer *et al.* 2009) and sometimes certain food items may have social, political or symbolic benefits in addition to the energy they contain and their chemical composition (Hockett 2015; Jones *et al.* 2013). OFT is thus enabling pre-historic human diets to be estimated (Dusseldorp 2012; Llano 2015), and hence increasing our understanding of observed remains of pre-historic meals (Dusseldorp 2012; Llano 2015; Sayers and Lovejoy 2014), and even the forces responsible for changes in our lifestyle (e.g., hunter-gatherer to agrarian) and social structure (e.g., origins of rulers, states, institutions etc) (Bird and O'Connell 2006; Codding and Bird 2015; Fuentes 2015). When modern-day developed-country infants, young enough to have had minimal exposure to observations of or information from others, are presented with a variety of seemingly 'natural' foods, they choose, when averaged over a day or longer, diets that may be considered 'balanced' in terms of both food types and energy consumed (Birch 1999; Pyke 1987; Savage *et al.* 2007). Studies, such as those described in this paragraph, remain relatively rare.

Human foraging behaviour is likely to be adapted to the foraging environment in a broader 'economic' sense, as foraging situations are generally similar or analogous to those we evolved to deal with and 'currencies' can be adopted for expressing relevant costs, benefits and risks. For example, both the Neolithic hunter-gatherer and the modern-day developed-world grocery shopper must decide whether, when and where to forage, and associated with the various alternatives there will be gains in terms of amounts obtained of different kinds of food, costs in terms of time, energy or equivalent (e.g., money), and risks of misadventure (e.g., getting lost or injured). In both situations, it would seem reasonable to hypothesise that individuals will 'weigh up' the alternatives and choose what appears best on the basis of some combined currency. Various aspects of foraging within present-day hunter-gatherer societies, in addition to diet, have been found to be consistent with expectations based on OFT (Bird and Bird 1997; Lupo 2006; Thomas 2007b). Foraging choices by grocery-store shoppers are influenced by factors such as travel times to alternate stores, available items and associated information, socio-economic variables, prices, promotions, and how items are presented (Anderson *et al.* 2000; Lusk *et al.* 2006; Oliveira-Castro *et al.* 2006; Sentyrz and Bushman 1998; Simpson 2006; Teng and Wang 2015; Vijaykumar *et al.* 2013; Webber *et al.* 2010; Zachary *et al.* 2013), but whether such choices can be considered optimal in any sense apparently remains little explored (Lieberman 2006). Other aspects of modern-day human foraging, including searching in general, accord with OFT (Dorn 1997; Hantula *et al.* 2008; Pires and Clarke 2011; Schoville and Otarola-Castillo 2014).

In other words, human foraging behaviour may be generally optimal, though determined by complex sets of interacting processes, and further research seems warranted.

Zoology on the Table

Because we evolved as omnivores, animal meat is likely to remain 'on the table' indefinitely, but amounts consumed will no doubt depend on availability, benefits – both real and imaginary, and costs – also possibly real and imaginary, all of which are the basic ingredients of the optimal foraging approach, as explained above. In general, consistent with OFT expectations, amounts of consumed animal meat should increase with increases in availability and perceived benefits and with decreases in associated costs, and decrease when the opposite trends occur (Pyke *et al.* 1977).

Of course, the perceived benefits of consuming animal meat will be influenced by how we feel at the prospect of eating meat or when we eat or have eaten various animal meats, and hence we are likely to be greatly influenced through what we hear or see via others, especially by way of advertising and marketing. To many, myself included, most available animal meat, including from some invertebrates, is wonderfully enjoyable and nutritious to eat in appropriate amounts; some others reject eating meat from animals, often including invertebrates, and obtain their dietary protein from plant-based sources (Lund and Olsson 2006; Ruini *et al.* 2015). Advertisements have been cast in both directions, and the same issues have arisen in the context of using other animal products.

Anyone wishing to see changes in the amounts of animal meat we consume should probably seek to promote such ideas through personal influence and advertising, possibly enlisting people with high positive profiles for promotion and presentation. A good example can be seen in the approach taken by the group *People for the Ethical Treatment of Animals* (*PeTA*) which has enlisted a number of 'celebrities' to help promote a vegetarian or vegan lifestyle (see http://www.peta.org/features/2016-sexiest-veg-celebrities/; accessed July 2016).

Those, like me, who are concerned about negative impacts of food advertisement, especially those arising from over-consumption of fats, oils, sugar and salt, should hope or campaign for appropriate government action, including regulation concerning honesty and disclosure of information in advertisements, and programs to encourage and facilitate 'healthy living'. Some steps in such directions have been taken, but more can be done.

Where to from here?

Looking ahead, I imagine that there will be further research in terms of OFT in the context of foraging by non-human organisms and extensions to other areas of biology, using OFT to understand human archaeology and anthropology, and understanding human dietary choice. Despite the 50-year long history of OFT, interest in it continues to grow (Pyke 2010b). Interest in applying OFT to archaeology and anthropology has recently increased markedly (Bird 2015; Codding and Bird 2015; Fuentes 2015). There is ongoing interest in understanding human dietary choice, especially in relation to mitigating the increasing development and maintenance of choices with adverse health impacts (Birch and Doub 2014; Lopez and Knudson 2012; Raubenheimer et al. 2015; Savage et al. 2007). However, it seems unlikely that there will be much additional attempt to understand the biological basis of foraging choices we humans make, other than the items we select as we stroll down the aisles of the grocery store, or in other contexts of commercial interest.

It seems also likely that there will be ongoing research on the effectiveness of advertisement and marketing, especially in relation to our diets, and we shall continue to be deluged with advertisements and the like telling us what we should eat and drink. The effectiveness of advertisement and marketing is of obvious commercial interest, both to those who provide us with dietary options and those who seek to promote certain dietary choices (Simpson *et al.* 2015). The deluge of advertisements will continue, simply because they work, often well.

Finally, I imagine that 'zoology on the table' will continue to be a vexed and much discussed issue, and hope that my discussion in this article will prove useful and helpful, providing optimal 'food for thought'.

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